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Terpenoids and Plant Communication

Joan Llusià, Marc Estiarte & Josep Peñuelas*

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Abstract

Terpenoids are compounds containing an integer number of 5C units, the «syllables». There is an astonishing array of structures, the «words», resulting from the sequential combination of these basic five-carbon units in the familiar categories of C10 (mono-), C15 (sesqui-), C20 (di-), C30 (tri-) C40 (tetra-) and C>40 (poly-) terpenoids. Terpenoids are induced and emitted in response to internal (genetic and biochemical) and external (ecological) factors, both abiotic and biotic. They are emitted in quantitatively and qualitatively diverse blends, the «messages», that arrive to the environment either through volatilization (mono- and sesquiterpenes), leaching or decomposition of plant debris. Their information or effect is received and responded by other parts of the plant, other plants, animals and microorganisms.
Part of such terpenoid «words» are common to all plants. For example, carotenoids, chlorophylls or hormones such as cytokinins, gibberellins, or abscicic acid, are terpenoid derivatives. But there are also «dialects» of the terpenoid «language» that are qualitatively or quantitatively characteristic of each family and each species, or even each cultivar and each organ of the plant. They even seem to be kept in «memory». Some plants might remember previous exposures and produce terpenes (and compounds of other chemical languages such as phenolics or alkaloids) when they are needed. Thus, plants also have languages, and that of terpenoids is one of them.

*Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Facultat de Ciències, Universitat Autònoma, E-08193 Bellaterra, Barcelona.

KEYWORDS: Terpenoids, plant language, plant-plant, plant-animal and plant-microorganism communication, memory.

Resum

Els Terpenoids i la comunicació vegetal

Els terpenoids són compostos que contenen un nombre integral de cinc unitats de carboni, les «sil·labes». Hi ha un sorpenent nombre d'estruc-tures, les «paraules», que resulten de la combinació seqüencial d'aquestes unitats bàsiques de cinc carbonis en categories de C10 (mono-), C15 (sesqui-), C20 (di-), C30 (tri-), C40 (tetra-) i C>40 (poli-) terpenoids. Els terpenoids són induïts i emesos en resposta a factors interns (genètics i bioquímics) i externs (ecològics), tant abiòtics com biòtics. Són emesos en barreges quantitativament i qualitativa diverses, els «missatges», els quals arriben a l'ambient a través de la volatilització (mono- i sesquiterpens), la lixiviació, o la descomposició de les restes vegetals. La seva informació és rebuda per altres parts de la planta, per altres plantes, per animals i per microorganismes.
Algun d'aquests terpenoids («paraules») són comuns a totes les plantes. Per exemple, els carotenoids, les clorofil·les o hormones com ara les citoquinines, les giberelines o l'àcid abscísic són derivats terpènics. Però també hi ha «dialectes» del «llenguatge» dels terpens que són qualitativament o quantitativament característics de cada família i de cada espècie, i sovint de cada cultivar i de cada òrgan de la planta. Fins i tot sembla ser que algunes plantes recorden exposicions prèvies i produeixen terpens (i compostos d'altres llenguatges químics com els dels fenols o els dels alcaloides) quan els necessiten. Per tant, les plantes també tenen llenguatges i el dels terpenoids n'és un dells.

MOTS CLAU: Terpenoids; llenguatge vegetal; comunicació planta-planta, planta-animal, planta-microorganismes; memòria.

Resumen

Los terpenoides y la comunicación vegetal

Los terpenoides son compuestos que contienen un número integral de cinco unidades de carbono, las «sílabas». Existe un sorprendente número de estructuras, las «palabras», que resultan de la combinación secuencial de estas unidades básicas de cinco carbonos en categorías de C10 (mono-), C15 (sesqui-), C20 (di-), C30 (tri-), C40 (tetra-) i C>40 (poli-) terpenoides. Los terpenoides son inducidos y emitidos en respuesta a factores internos (genéticos y bioquímicos) y externos (ecológicos), tanto abióticos como bióticos. Son emitidos en mezclas cuantitativa y cualitativamente diversas, los «mensajes», los cuales llegan al ambiente a través de la volatilización (mono- y sesquiterpenos), la lixiviación, o la descomposición de los restos vegetales. Su información es recibida por otras partes de la planta, por otras plantas, por animales y por microorganismos.
Alguno de estos terpenoides («palabras») son comunes a todas las plantas. Por ejemplo, los carotenoides, las clorofilas, algunas hormonas como las citoquininas, las giberelinas o el ácido abscísico son derivados terpénicos. Pero también existen «dialectos» del «lenguaje» de los terpenos que son cualitativamente o cuantitativamente característicos de cada familia y de cada especie y, a menudo, de cada cultivar y de cada órgano de la planta. Incluso parece ser que algunas plantas recuerdan exposiciones previas y producen terpenos (y compuestos de otros lenguajes químicos como los de los fenoles o los de los alcaloides) cuando los necesitan. Por tanto, las plantas también tienen «lenguajes» y el de los terpenoides es uno de ellos.

PALABRAS CLAVE: Terpenoides; lenguaje vegetal; comunicación planta-planta, planta-animal y planta-microorganismos; memoria.

Introduction

Increasing recognition of the ecological importance of terpenoids is reflected by the several recent reviews of the ecological chemistry and role of terpenoids (Harborne, 1991; Gershenzon & Croteau, 1991; Lerdau & Peñuelas, 1993; Langenheim, 1994; Gershenzon, 1994). A defensive role has persistently been presented as the main role and the function of secondary compounds, including terpenoids, since the field of chemical ecology developed essentially arround the concept of coevolution (Feeny, 1992). However, the fact that higher plant terpenoids result in mediation of numerous kinds of ecological interactions makes them also act as infochemicals (Dicke & Sabelis, 1988). There is also a lively debate on the ecological and evolutionary significance of plant communication (Langenheim, 1994; Bruin *et al*., 1995). We have proposed to merge both subjects, terpenoids and plant communication, by approaching terpenoids as a chemical «language» of plants (Peñuelas *et al*., 1995a). Here we present the development of such approach. Terpenoids are emitted in response to internal and external factors, and their information or effect is received and responded by other parts of the plant, other plants, animals and microorganisms. A survey of recently recorded ecological effectivity of terpenoids shows it to be concentration or dosage dependent (Harborne, 1991). For example, biological reaction of insects to terpenoids characteristically is one of attraction or stimulation at low concentrations, with the

response becoming increasingly of repellence or inhibition as the concentration increases (Lovett, 1989).

«Syllables, words and messages»

Terpenoids are compounds containing an integral number of 5C units. We can consider those units as the «syllables». There is an astonishing array of structures resulting from the sequential combination of basic five-carbon units in the familiar categories of C10 (mono-), C15 (sesqui-), C20 (di-), C30 (tri-) C40 (tetra-) and C>40 (poly-) terpenoids, which we can consider the «words». Both the number and structural diversity of terpenoids provide enormous potential for mediating significant ecological interactions. They are emitted to the environment either through volatilization (mono- and sesquiterpenes) (Seufert *et al*., 1995), leaching or decomposition of plant debris (White, 1994). They are emitted forming qualitatively and quantitatively diverse blends with additive sinergic or antagonic effects (Asplund 1969; Fischer *et al* 1988; Langenheim, 1994), which we can consider the «messages».

«Common language and dialects»

Part of such terpenoid «words» are common to all plants. For example photosynthesis depends on the existence of certain terpenes and terpenoid derivatives (carotenoids and chlorophylls). Besides, many hormones such as cytokinins, gibberellins, abscicic acid and, possibly, the xanthoxins are terpenoid derivatives.

But there are also «dialects» of the terpenoid «language» that are characteristic of each family and each species or even cultivar (Takabayashi *et al*., 1994). The different relative proportions of the constituents in the emitted mixtures have considerable ecological consequences (Langenheim, 1994). They play an important role in plant communication. They are induced in response to internal (genetic and biochemical) and external (ecological) factors and to both, abiotic and biotic factors, and they get a dosage dependent response (Langenheim, 1994). Like in any other language, the «dialects» or particular terpenoid classes characterize certain plant-families (Takabayashi *et al*., 1994). They also vary qualitative and quantitatively intraspecifically (reviewed by Langenheim, 1994 and Takabayashi *et al*., 1994). They even vary qualitatively and quantitatively among organs and during organ development (Langenheim *et al*., 1978; 1986). There is thus an enormous diversity of terpenoids.

Plant terpenoid content and emission

Although terpenoids contents are in the range of 1-2 % dry weight, they can attain 15-20 % plant dry weight (Langenheim, 1994). Terpenoid content and emission respond to abiotic and biotic factors. There are increases with light or CO_2, and decreases with fertilization (our group, unpublished data). Decreases of 42 % of total amount of monoterpenes have also been reported during the summer months in *Picea abies* (Kotzias *et al*., 1992). The same authors found little seasonal changes in relative proportions, but other reports have shown seasonal modifications (Gershenzon & Croteau, 1991). On the contrary, emission of isoprene, the 5C unit, has been linked to protection against higth temperatures (Sharkey & Singsaas, 1995). The emission of isoprene has also been shown to be linked to the photosynthetic processes of the chloroplasts (Sharkey *et al*., 1991). Sometimes the changes have been related to herbivory pressure (Takabayashi *et al*.,

1994). There can even be a possible role of biotic selection pressures in determining the distribution of plant terpenoids (Lincoln & Lagenheim, 1978).

Internal communication (an immune system)

Portions of the plants seem to be able to communicate with the other parts. For example, the existence of some sort of internal communication system whereby damaged portions of the plant rely information to other undamaged portions has been suggested in the attack of entomophagous insects (Dixon & Payne, 1980; Elzen *et al*.,1984; Turlings *et al*., 1991). Turlings & Tumlinson (1992) propose that terpenoids may even provide a plant an equivalent to an immune system, an idea further supported by Takabayashi & Dicke (1993).

Plant-plant communication

Alarm against herbivores

There is behavioral and chemical evidence for the involvement of the host plant in production of volatile allelochemicals upon damage by herbivores, with the consequence of attracting herbivore predators (Takabayashi *et al*., 1994). These volatiles not only influence predator behavior, but also prey behavior and also the attractiveness of nearby plants to predators. Herbivorous mites, for example, disperse away from places with high concentrations of the volatiles, and undamaged plants attract more predators when previously exposed to volatiles from infested conspecific plants rather than from uninfested plants, thus influencing the plant population beyond those being attacked (Bruin *et al*., 1992, 1995). There seems thus to exist plant-plant communication (Dicke *et al*., 1990).

Allelochemicals and allelopathy.

Reese (1979) used the term «allelochemical» to describe «non-nutritional chemicals produced by one organism that affect the growth, health, behavior or population biology of other species». Allelopathy is identified particularly with chemical activity between plants (Kolzowski *et al*., 1991); however, entomologists refer to allelopathy in a broader sense as the communication between plants and other organisms. Allelopathic roles are often ascribed to mono- and sesquiterpene messages. Terpenoid toxicity results from several effects such as inhibition of ATP formation, alkylation of nucleophiles, disruption of hormonal activity, complexation with protein, binding with free sterols, inhibition of respiration, or increasing relative electron partitioning to the alternative oxidase pathway (Peñuelas *et al*., 1995b). Allelopathic effects seem particularly evident in Mediterranean and desert climates (Friedman, 1988).

Studies of plant-plant chemical interaction through allelopathy have often been controversial because of difficulty in unambigously demonstrating interference by chemical inhibition rather than through resource competition or other mechanisms (Harper, 1977). However, Fischer (1991) pointed out that it has long been known that essential oils and individual monoterpenes strongly inhibit seed germination and plant growth. Fischer *et al.* (1988) showed selective action of monoterpenoids within a community (e.g. cineole was highly toxic to one grass but not to others) and seasonal variations in inhibition of germination and growth (highest levels occurring during June and July), and high inhibitory effects of terpene mixtures on germination contrasting with stimulatory effects of pure terpene solutions, which suggests strong

synergistic effects. Similar results had been reported by Asplund (1969). However, Peñuelas *et al*. (1995b) have found clear inhibitory effects of pure α-pinene on plant respiration.

Plant-insect communication

Volatile compounds are used by insects for social communication. Therefore, insects can become sensitive to similar molecules emitted by plants such as the terpenoids (Harborne, 1993). In a mixture of terpenoids emitted by a plant, some may be feeding stimulants for adapted specialist herbivores whereas others or the same may be toxic or deterrent for non-adapted herbivores. This deterrence has been applied to the management of insect infestation (Salom & Hobson 1995). Some insects specialize on terpenoid-producing plants even to the extent of exploiting the terpenoid molecules themselves. There are complex relations e.g. some conifer species benefit at one life stage of diprionid sawflies, whereas the insects benefit at another stage of plant diterpenes (Larsson *et al*., 1986). Among these complex plant-insect commu-nication interactions, the following repellent and attracting ones are some of the better known.

Alarm pheromones

Some monoterpenoids may act as alarms signaling the plant as an unfavorable host. For example verbenone is released in increasing quantities as beetle attack progresses and thence completely inhibits the attractiveness of the host monoterpenes to the beetle (Byers *et al*., 1989). In fact, animal alarm pheromones have been isolated in aphids and identified as (E)–ß–pharnesene (Bowers *et al*., 1972) and (–)-germacrene A (Bowers *et al*., 1972, 1977a, 1977b, 1988; Nishino *et al*., 1977). (E)–ß–pharnesene is a terpenoid from leaves of the wild potato *Solanum berthaultii* Hawkes that is repellent to the aphid *Myzus persicae* (Sulzer) (Gibson *et al*., 1983).

Insect growth and sex regulators

Plants have also terpenoids that simulate insect growth and sex regulators in order to inhibit their development or their sexual activity. An example of insect growth regulators are the juvocimones, potent juvenile hormone mimics, discovered from *Ocimum basilicum* (Bowers & Nishida, 1980; Bowers, 1991). The hormonally active compounds from *O. basilicum* are obtained by distillation. These compounds possess exceedingly high juvenile hormone activity. They contain ocimene as a portion of their chemical structure. This is another proof of coevolution of insects and plants resulting in an incredibly complex chemical interaction. The presence of insect hormonal activity in plants was first demonstrated by Slama & Williams (1965) when they found that paper bathed with extracts of the balsam fir induced juvenilization of the linden bug *Pyrrhocoris apterus* (L). Some plants such as the Podocarpaceae produce substances that are inhibitory to insect development. Moreover, several plant-derived insecticide synergists, including sesamin and sesamolin, exhibit juvenile hormone activity against both beetles (*Tenebrio molitor*) and bugs (*Oncopeltus fasciatus*).

Several plant extracts reproduced the intense courtship and mating behaviour induced by the natural sex pheromone of the american cockroach, *Periplaneta americana* (Bowers & Bodenstein, 1971). The active compounds were simple terpenes including (+)-bornil acetate, α and ß-santalol, and an unidentified $C_{15}H_{24}$ hydrocarbon (likely germacrene D, Tahara *et al*., 1975).

Herbivore-induced synomones (Indirect defense)

There is also an indirect plant defense through the attraction of entomophages. Plants produce volatile allelochemicals upon damage by the herbivores with the consequence of attracting predators. Terpenoids behave thus as synomones, substances that enhance the effectiveness of natural enemies of herbivores (Takabayashi *et al*., 1994). This phenomenon is termed «indirect defense», which may be induced by herbivore damage («herbivore-induced synomone», HIS). The HIS vary among different plants species, depending upon: a) plant cultivar, b) leaf growth stage, c) the herbivore species that is attacking, and d) abiotic conditions (light intensity, time of year, and water stress).

Attraction, and aggregation

Terpenoids are also used by plants to attract pollinators. Some terpenoids are commonly found in flower odors (Knudson *et al*., 1993), sometimes with dayly rithmicity as in flowers pollinated by night-flying insects and bats (Dobson, 1993).

Conifer monoterpenes are also involved in beetle host-finding. In fact, aggregation pheromones frequently are allylic oxidation products of host monoterpenes (Wood, 1982).

Plant-other organisms communication

Mammals

There is also a complex and not well known response of mammals to plant scents (Peñuelas, 1993). There are some evidences that terpenes could in some cases inhibit digestion of hares and deer through odor deter based on quantity more than quality. Dietary monoterpenes could be toxic to ruminants by supressing the activity of their digestive microorganisms (Oh *et al*., 1967). However, some recent studies in vivo have suggested that monoterpene concentrations in the rumen of deer and rabbits appear to be lower than those used in «in vitro» studies and perhaps too low to interfere with microbial digestion (White *et al*., 1982), may be because of their volatility.

Fungi

Terpenoids are also defenses against insect-vectored fungi and potentially pathogenic endophytic fungi such as described in coastal redwoods (Espinosa-García *et al*., 1993). There is rapid de novo synthesis of resin near the site of infection vectored by beetles. The induced resin often has a different monoterpenoid composition than the constitutive resin (Raffa & Klepzig, 1992). Generally, those terpenoids of constitutive resins that occur in greatest quantities are induced the least, whereas the rarer monoterpenes are induced in larger quantity. In general there is a disproportionately high increase in those chemicals that have the most deleterious effects on insects and fungi during the induced response (Raffa, 1991). However, there are also reports of terpenes having no significant effect on hyphal growth of *Alternaria alternaria* and *Botrytis cinerea* (Hamilton-Kemp, *et al*., 1992).

Microorganisms

Plant-microorganism communication also presents all kinds of repellent and attracting interactions. Monoterpenoids defensive effects have been documented in bacteria and yeast (Andrews *et al*., 1980). Terpenoids in the soil may inhibit some bacteria or provide energy source for others, and may have significant consequences on nutrient cycling (White, 1994). Monoterpenes could potentially interact with herbivory,

decomposers, N mineralization, N immobilization, nitrification, denitrification, and N fixation, thus having important effects on N cycling (White, 1994).

Network of communication

Terpenoids may then be considered as a «language» in the «network of chemical communication» between plants and other organisms. Plants produce terpenes and other chemical languages such as phenolic or alkaloid compounds for example once a plant has been attacked by an herbivore. It takes some minutes or some hours to get the actual response, but this is not too slow compared to the feeding rates of invertebrate hervivores. It would be like a plant immune system. Plants could remember previous exposures to pathogens or herbivores, and respond faster to the next attack or interaction.

In conclusion, plants may be able to communicate among themselves and with other organisms through chemical languages. The language of terpenoids constitutes one of the most versatile of these chemical languages.

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